A preliminary investigation of the phenology of subtropical thicket and karroid shrubland in the lower Sundays River Valley, SE Cape

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I studied the phenology of a range of growth forms in four vegetation types along an aridity gradient in the lower Sundays River Valley to test two phenology models for semi-arid ecosystems. As aridity increased along the gradient, phenological activity became concentrated within a shorter period. For the most arid site, in the Central Lower Karoo, the data favour Noy-Meir's (1973) view of a 'pulse-activity' phenological response to unpredictable rainfall. In the subtropical thicket communities, geophytes, lianes and leaf and stem succulents — all growth forms which contain water storage abilities — generally grew independently of seasonal rainfall. Communities with a greater number of species with adaptations for water storage generally showed a higher incidence of species which grew outside of the main rainfall period.

Ek het die fenologie van 'n reeks groeivorme in vier plantegroeitipes langs 'n ariditeitsgradiënt in die laer Sondagsriviervallei bestudeer, om twee fenologiese modelle vir semi-ariede ekosisteme te toets. Soos die ariditeit langs die gradient toeneem, word fenologiese aktiwiteit binne 'n korter periode gekonsentreer. Vir die mees ariede perseel in die sentrale laer Karoo, onderskryf die data Moy-Meir (1973) se siening van 'n 'polsaktiwiteit'-fenologiese reaksie op onvoorspelbare reënval. In die subtropiese struikgewasgemeenskappe, groei geofiete, liane en blaar- en stamsukkulente — almal groeivorme wat oor waterbergingsvermoë beskik — in die algemeen onafhanklik van seisoenale reënval. Gemeenskappe met 'n groter aantal spesies wat aanpassings vir wateropberging besit, vertoon oor die algemeen 'n hoër insidensie van spesies wat buite die hoofreënvalperiode groei.

Keywords: Gradient, Karoo, phenology, semi-arid, subtropical thicket

Introduction

There exist only a few detailed studies on the phenology of semi-arid vegetation of South Africa (Roux 1966, 1968; Liversidge 1972; van Rooyen *et al.* 1979a, b; Palmer 1982; Pierce & Cowling 1984; Le Roux *et al.* 1984; Tinley 1985). Such studies, however, contribute to an understanding of the organization of organisms, communities and ecosystems (Frankie *et al.* 1974) and often form the rationale for management systems (e.g. Acocks 1966; Roux 1968; Walker *et al.* 1986).

Noy-Meir (1973) outlines three main attributes of semi-arid and arid ecosystems. Firstly, he suggests that precipitation is low and water is the '... dominant controlling factor for biological processes' in these areas; secondly, precipitation is variable; and thirdly, this variability has a large unpredictable component. As a result, Noy-Meir (1973) suggests that the phenology of all species, whether ephemeral or perennial, of arid and semi-arid systems is characterized by a pulse-activity response to unpredictable rainfall events. He suggests that phenology within these systems may be described as a 'pulse-and-reserve' model (see Noy-Meir 1973) and considers these systems 'event-driven'.

For the Karoo, a semi-arid and arid dwarf shrubland, covering a third of South Africa's land surface, Roux (1968) proposes that different growth forms and species respond to rain at different times of the year. Grasses, he suggests, are 'primarily stimulated and favoured' by summer rains (i.e. September–February) and shrubs are 'invigorated' by winter rains (i.e. autumn, winter and early spring). Roux's (1968) emphasis is therefore on the seasonal specialization of growth forms and species. His model suggests that different species and growth forms have distinct periods of activity throughout the year and that they are relatively predictable from year to year.

I studied the phenological responses of a range of growth forms in four vegetation or veld types (Acocks 1953) along an aridity gradient in the lower Sundays River Valley to test these two models for semi-arid systems. In particular, I was interested in determining if subtropical thickets and karroid shrublands have a different phenological response to precipitation and what the range of responses within the subtropical thickets were. I show that as aridity increases, phenological activity becomes concentrated within a shorter period and that in the Central Lower Karoo a pulse-activity response to rainfall occurs.

Methods

Study area

The south-eastern (SE) Cape is a physiographically complex region comprised of a series of dissected lands. There are four major river systems in the region, all bounded by the watershed of the Great Escarpment. This study is concerned with the lower portion of the westernmost basin, the Sundays River Valley, which occupies the most arid part of the SE Cape. Although the Central Lower Karoo study site does not form part of the lower Sundays River Valley drainage system proper, it occurs on the Karoo Plains (see Hoffman 1989; Hoffman & Cowling 1989) which skirt the valley to the west and north.

Three veld types (Acocks 1953) with Tongaland–Pondoland regional mosaic affinities (White 1983) — Sundays River Scrub, Addo Bush and Noorsveld — comprise the subtropical thicket component (Cowling 1984; Lubke *et al.* 1986; Everard 1987) (Table 1). The main structural features and dominant species of these thickets are given in Table 1. They are physiognomically similiar to other floras of the river valleys of the eastern seaboard of southern Africa. These 2-m to 4-m tall subtropical thickets of the lower Sundays River Valley are characterized by a high incidence of succulence and spinesence (Acocks 1953) especially in the Noorsveld which is dominated by the stem succulent *Euphorbia coerulescens* Haw. Lianes [e.g. *Rhoicissus* spp., *Kedrostis nana* (Lam.) Cogn.] and parasites [e.g. *Viscum* spp., *Moquinella rubra* (Spreng. f.) Balle] are common, especially in more mesic sites.

Central Lower Karoo (Acocks 1953) vegetation comprises a dwarf and open, semi-arid shrubland and interdigitates with the Noorsveld (Acocks 1953). It is dominated by deciduous and evergreen shrubs and annual and perennial grasses. Geophytes, annual herbs and lianes form a minor component of this veld type.

There exists an aridity gradient from coastal to inland sites (Table 1). A detailed analysis of the physiography and climate of the region is contained in Hoffman (1989) and Hoffman & Cowling (1989).

Moisture

Total monthly rainfall records were taken from the closest weather station. These stations were: Central Lower Karoo–Klipplaat SAR (Station No 52/571, situated 9 km from the study site); Noorsveld–Lake Mentz (Station No. 54/253, 28 km from the study site); Addo Bush–Addo-Citrus Research (Station No. 35/334, 22 km from the study site); Sundays River Scrub–Uitenhage-Springs (Station No. 34/762, 1 km from the study site).

Monthly mean percentage soil moisture contents were determined gravimetrically from four samples in each veld type at each of two depths (0–50 mm; 100–150 mm). I chose these depths since soils at the Central Lower Karoo site were generally shallower than 200 mm and contained most root material in the first 150 mm.

Phenology

A homogenous and representative sample of relatively undisturbed vegetation in each veld type was subjectively chosen. At monthly intervals from November 1985 to November 1986 I examined individuals of different species in a 3- to 4-h period in an area of about 1 ha at each site, and recorded their phenological status. The same individuals were not necessarily studied each month but were chosen at random from the community. The number of individuals examined depended on the abundance of the species in the community. For each individual I recorded the presence or absence of new leaf and shoot growth, flower buds and flowers, immature and mature fruits, leaf yellowing and leaf abscision. I considered a species to be in a particular phenophase if two or more individuals were in it. Based on these observations, phenodiagrams for each species (December 1985 to November 1986 only), growth form [categories of Cowling (1986)] and community were constructed.

Results

Moisture

Precipitation and percentage soil moisture contents

Table 1 Environmental and vegetation characteristics of four stations along an environmental gradient in the lower Sundays River Valley and adjacent Karoo

Site	Location	Vegetation[1]	Structural characterization[2]	Dominant species	Altitude (m)	Rainfall[3] annual (mm)	Temperature[3] annual (°C)
1	Springs Nature Reserve 33°42′S 25°25′E	Sundays River Scrub	Tall closed large-leaved shrubland (with a sparse succulent low tree overstorey)	*Capparis sepiaria, Euclea undulata, Portulacaria afra*	150	469	13.8
2	Farm: Brakleegte 33°33′S 25°28′E	Addo Bush	Tall closed large-leaved and succulent shrubland	*Euclea undulata, Euphorbia ledienii, Grewia robusta*	300	381	15.0
3	Farm: Gannahoek 33°14′S 24°53′E	Noorsveld	Low mid-dense succulent shrubland (with a sparse mid-high and tall large-leaved shrub overstorey)	*Euphorbia coerulescens, Pentzia incana, Rhigozum obovatum*	550	294	15.3
4	Farm: Teasdale 33°06′S 24°18′E	Central Lower Karoo	Dwarf and low open Graminoid and small-leaved shrubland	*Enneapogon scoparius, Pentzia incana, Selago albida*	600	230	15.9

[1]Acocks'(1953) veld types

[2]after Campbell *et al.* (1981)

[3]data from Weather Bureau

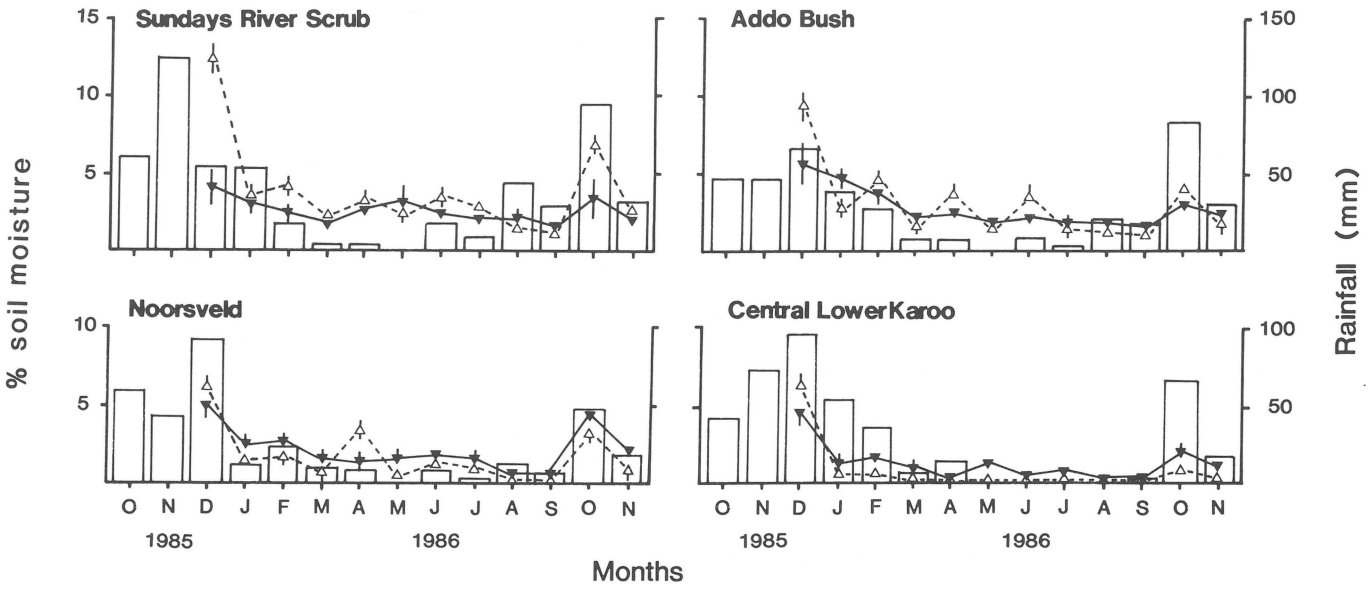

Figure 1 Monthly rainfall (bars) and soil moisture content (dashed line = 0–50 mm depth; solid lines = 100–150 mm depth) at four study sites in the lower Sundays River Valley and adjacent Karoo. Precipitation was recorded at the nearest weather station (see text for station names, station numbers and distance from study site).

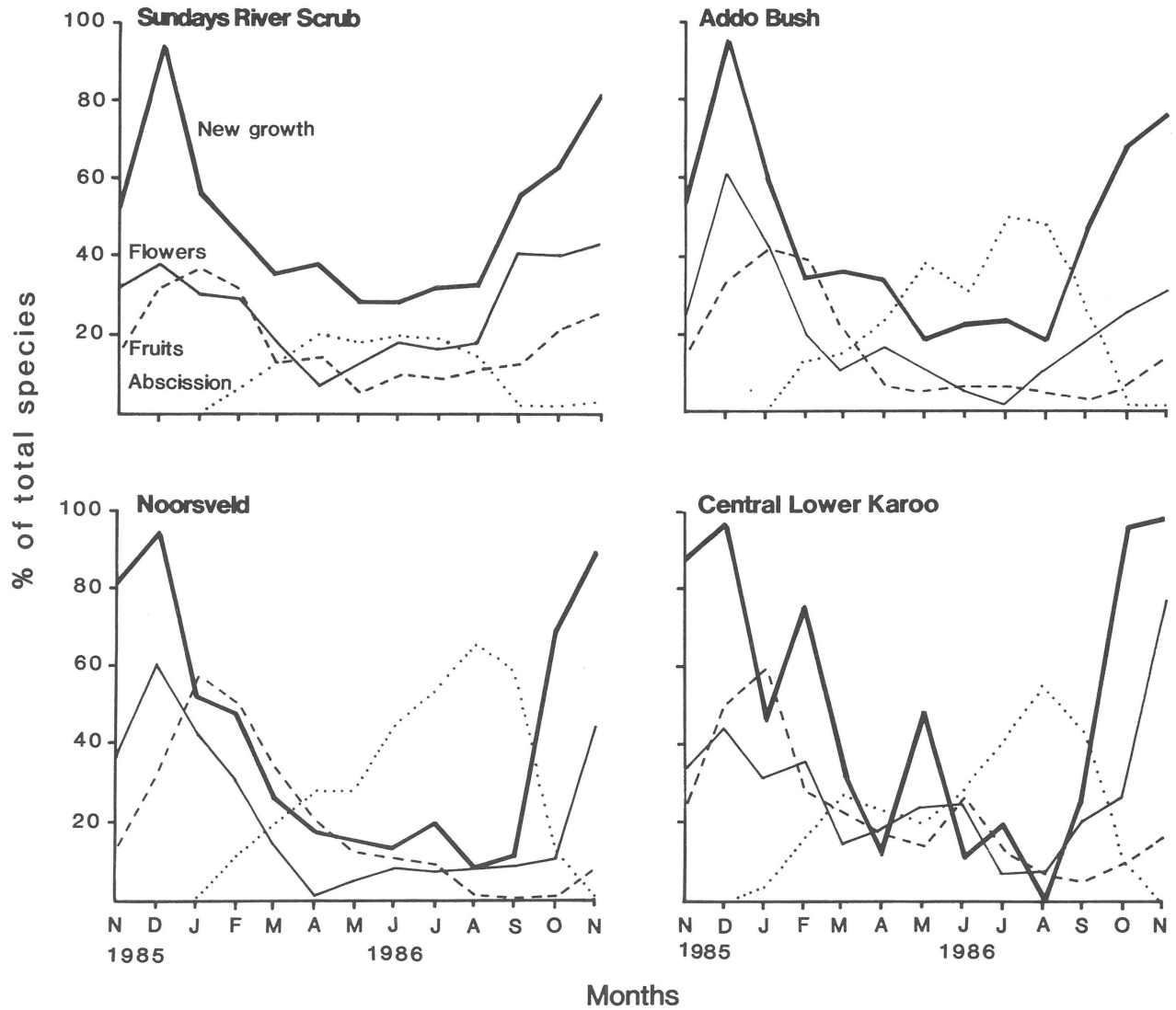

Figure 2 Community phenologies of four veld types along an aridity gradient in the lower Sundays River Valley and adjacent Karoo.

showed seasonal variation, peaking in summer (1985) and spring (1986) for all stations (Figure 1).

Community phenology

Growth patterns were similiar in Sundays River Scrub, Addo Bush and Noorsveld communities; nearly all species showed a summer growth peak (Figure 2). However, there was less growth activity outside of the summer period in Noorsveld than in Sundays River Scrub and Addo Bush vegetation. As aridity increased, phenological activity became more concentrated within a shorter period.

A different phenological pattern was evident in the Central Lower Karoo (Figure 2). This was characterized by pulses of growth, flowering and fruiting. The 16.5 mm of rain which fell at the end of April 1986 resulted in a marked growth response from some grasses (e.g. *Eragrostis bicolor* Nees, *Aristida diffusa* Trin.) and some shallow-rooted (< 200 mm) shrubs [e.g. *Pentzia incana* (Thunb.) Kuntze, *Plinthus karooicus* Verdoorn]. The growth peak in July occurred largely as a result of new growth in leaf succulents (*Drosanthemum* spp., *Eberlanzia* spp.) and that in September as a result of new leaf growth in geophytes (*Albuca* sp., *Ornithogalum prasinum* Lindl.).

Growth form and species phenology

The four veld types comprise a diverse array of growth forms and there were few consistent generalizations about phenology for each growth form for all sites (Appendix 1). However, within the subtropical thickets, grasses and annuals showed short growth periods. Geophytes, which showed low flowering and fruiting levels, appeared to grow asynchronously with rainfall peaks at all subtropical thicket sites. All lianes possessed underground water storage organs and growth, flowering and fruiting extended over long periods, as did those for parasites. Deciduous and evergreen subtropical thicket shrubs appeared restricted to summer growth activity. Flowering and fruiting levels were low but often spread over several months so that at any one time at least a few species were in flower or fruit. Leaf succulent shrubs appeared to grow throughout the year but with summer peaks apparent. Stem succulent shrubs exhibited summer–autumn growth peaks and an absence of flowers or fruits over the colder winter months.

For the Karoo, growth appeared correlated with soil moisture. There existed a continuum, from briefly photosynthetically active, to apparently continuously active elements between growth form categories. Geophytes and annuals, for example, produced leaves very briefly in response to rain (Appendix 1). Some evergreen shrubs (e.g. *Aptosimum indivisum* Burch. ex Benth., *Helichrysum pentzioides* Less., *H. zeyheri* Less.), on the other hand, appeared to lose only a few leaves throughout the year, without a single period of great leaf loss. When rains greater than 25 mm fell, leaf exchange was not entire. There was considerable variation between these two extremes. Some deciduous shrubs [e.g. *Lycium cinereum* Thunb. (*sens. lat.*), *Selago albida* Choisy] and leaf succulents (e.g. *Drosanthemum* spp.) responded rapidly to rain. Growth was short-lived and leaf abscision equally rapid in some of these species. Other deciduous shrubs [e.g. *Felicia filifolia* (Vent.) Burtt Davy, *Pentzia incana* (Thunb.) Kuntze, *Rosenia humilis* (Less.) Bremer, *Sutera atropuperea* (Benth.) Kuntze], maintained their leaves, which progressively turned either red or yellow. They were not dropped immediately it became dry. How long they remained photosynthetically active, however, is unknown. With the onset of rain, all these 'old' leaves were dropped over a very short period and replaced by new growth.

All growth forms in the Karoo, except geophytes and stem succulents and to a lesser extent annuals responded to the late April rains. Even though all species grew in response to the summer rains of 1985 and 1986, some leaf succulents [e.g. *Eberlanzia cradockensis* (Runtze) Schwant., *Senecio acutifolius* DC.] showed signs of new growth in July. Two evergreen shrubs, *Helichrysum pentzioides* and *H. zeyheri* showed signs of active new growth in September 1986, before the October rain.

Discussion

There are qualitative differences in the phenology of subtropical thicket and karroid shrubland communities. Most subtropical thicket species exhibited summer growth peaks followed by a gradual diminution of growth activity. As aridity increased in the lower Sundays River Valley thickets, so did the trend to concentrate phenological activity within a shorter period. In contrast, there was a pulse-activity response to moisture in the Karoo. Karoo vegetation adhered more closely to the 'pulse-and-reserve' model of Noy-Meir (1973) than to the 'average growth cycle' model proposed by Roux (1968). There did not appear to be discrete periods of phenological activity for perennial grasses and shrubs as suggested by Roux's (1968) model.

In addition, these data depart somewhat from those of van Rooyen *et al.* (1979b) who showed that for the winter-rainfall, Succulent Karoo, species exhibited typical mediterranean-type phenological patterns with autumn and stronger spring growth peaks. Cold winters and hot, dry summers of the region limit growth in these seasons. Rain in the Nama-Karoo is less predictable (Rutherford & Westfall 1986; Hoffman & Cowling 1987) and species here may have evolved to exploit this unpredictable period largely irrespective of its seasonal occurrence. There appeared to be few species which showed endogenous rhythms in the Central Lower Karoo vegetation. However, phenological data collected over a 13-month period provides insufficient evidence to reject the view that these species show endogenous rhythms.

I found no evidence for the spring–autumn growth peaks reported by Liversidge (1972), Pierce & Cowling (1984) and Tinley (1985) nor for the midsummer leaf loss peak reported by Pierce & Cowling (1984) and Tinley (1985) for coastal thicket species. Two interpretations of these differences are possible. Firstly, while coastal and arid river valley thicket communities may be similar in

species composition, they may have different phenological patterns and may not be comparable. Tinley (1985) has noted that for coastal thicket species there is generally a year-round occurrence of fruit while strongly seasonal phenophases characterize the same adjacent arid valley thicket species. For the lower Sundays River Valley thickets it appears that seasonality becomes more pronounced as aridity increases.

Secondly, the patterns evident for the subtropical thickets in this study may merely be part of a more complex climate–phenology interaction. Tinley (1985) has linked the autumn–spring growth and reproductive peaks of coastal thicket species to an 'equinoctial reproductive strategy (which) enables plants to take advantage of any shift in the rainfall regime...'. This supports Pierce & Cowling's (1984) and Pierce's (1984) view that coastal thicket species have a generalist phenological strategy — i.e. whenever combinations of temperature and moisture are suitable then thicket species will grow. Although the extent of phenological plasticity (Pierce & Cowling 1984; Agami 1987) has not been determined for thicket species, Tinley (1985) suggests that it may be important in community phenological patterns. He notes that rain after a long drought may confer strong seasonality on community phenophases which change to a more aseasonal pattern again with year-round occurrence of rain. In view of this second argument, I speculate that my data may merely reflect a strongly demarcated summer response following the long drought of 1983/1984.

Environmental controls of leaf senescence in subtropical thicket trees and shrubs are probably more closely linked to dryness than daylength. The role of temperature is unknown. While some species shed leaves when days were shortening, a peak in this activity occurred approximately a month after the solstice in Addo Bush and approximately 2 months after the solstice in Noorsveld.

For the subtropical thicket communities, the phenology of geophytes, lianes and leaf and stem succulents — all species with water storage abilities — suggests that some species may grow independently of seasonal rainfall. The reallocation of stored metabolites and moisture may be activated by more predictable cues such as temperature or photoperiod. Generally, communities with a greater number of species with adaptations for water storage showed a higher incidence of growth outside of the main rainy periods. This has been interpreted as a means of partitioning resources between species, thereby reducing competition intensity and increasing species diversity (Kemp 1983; Pierce 1984). There is little difference in species diversity between the communities studied, even though the incidence of species with water storage abilities differs widely. The karoo community had the most species (60) yet the least (13) with specialized water storage organs. Phenological patterns of karroid species also show that, relative to subtropical thicket species, seasonal specialization is negligible. Temporal partitioning of resource exploitation amongst species, therefore, may not be an important determinant of semi-arid community alpha diversity, at least for sites in the lower Sundays River Valley. Rather, as Cody (1986) has suggested, morphology of root systems and the ability to partition the below-ground environment (Yeaton & Cody 1976) may be the most critical control of plant diversity. Although not studied in detail, it is evident that shallow-rooted shrubs in the Central Lower Karoo and subtropical thickets [e.g. *Walafrida saxatilis* (E. Mey.) Rolfe], responded consistently to smaller rainfall events in pulses of activity which were not apparent in other deeper-rooted species.

I have stressed that this study represents a preliminary investigation of the phenology of subtropical thickets and karroid shrublands. However, the suggestion that Central Lower Karoo vegetation exhibits a pulse-activity response to a relatively unpredictable moisture supply has considerable practical implications. Walker *et al.* (1986) have suggested that rainfall may be the most important driving variable in southern African rangelands and that competition and the effects of herbivory may be insignificant in comparison. These authors have proposed an event-orientated approach to grazing management and one which advocates the concentration of finances and labour during critical times '... when the system dynamics are most sensitive to such management.' Such an approach to management may be more appropriate in the Central Lower Karoo vegetation of the eastern Cape than the steady stocking rates and regular moves advocated under current management systems (e.g. Roux 1968).

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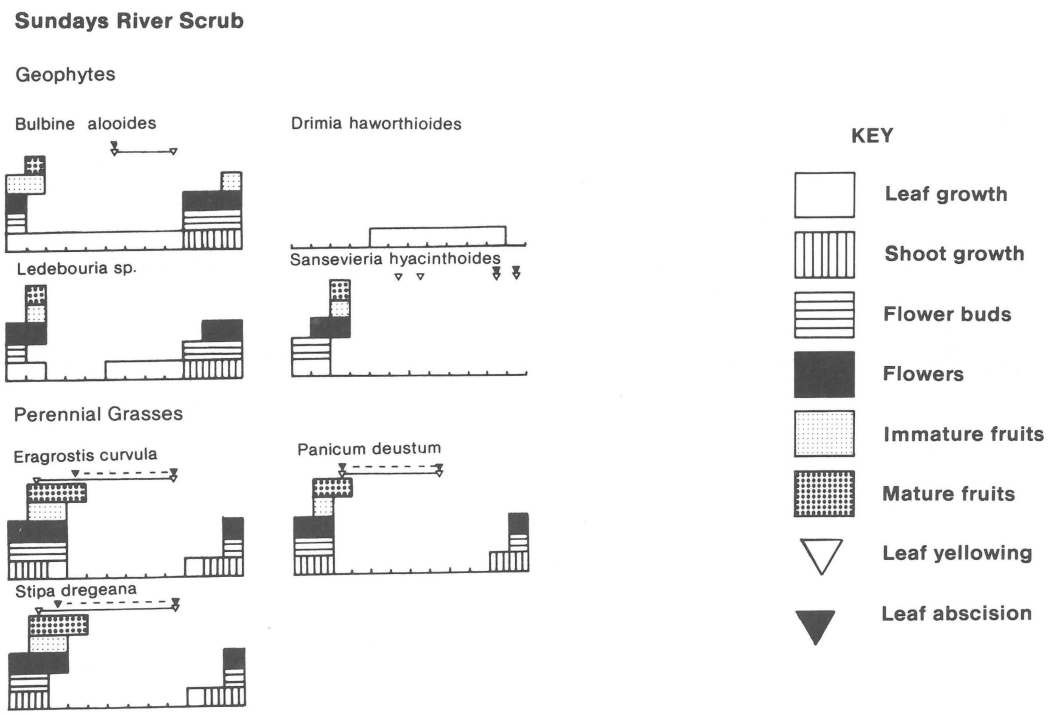
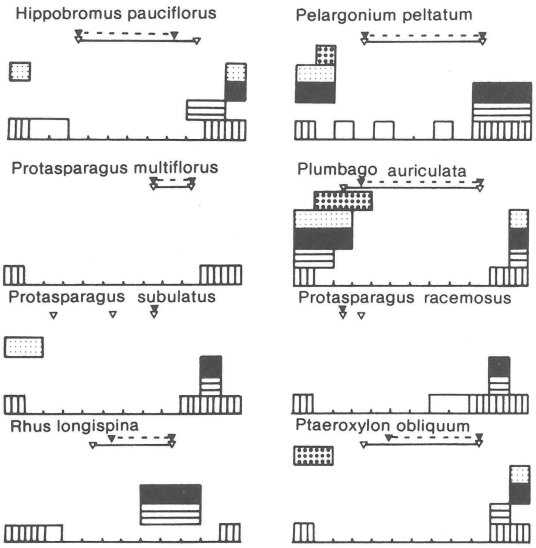
Appendix 1 Phenodiagrams for 228 species from December 1985 to November 1986 from four veld types in the lower Sundays River Valley and adjacent Karoo. Each division represents one month. Growth forms are those of Cowling (1986). Dwarf and low = < 1 m; mid-high and tall = 1– >2 m.

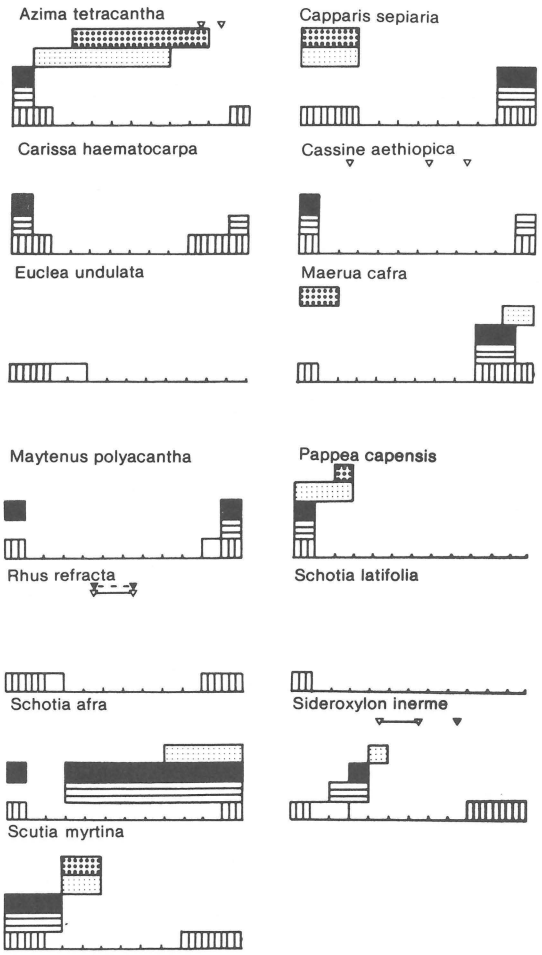


Appendix 1 Continued

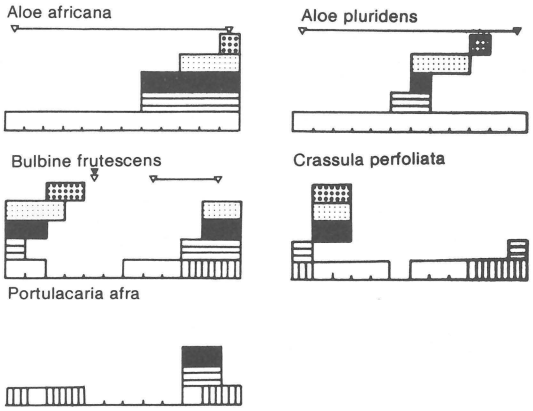
Mid-high and Tall Deciduous Shrubs



Mid-high and Tall Evergreen Shrubs



Mid-high and Tall Leaf Succulents



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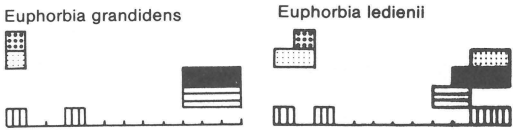
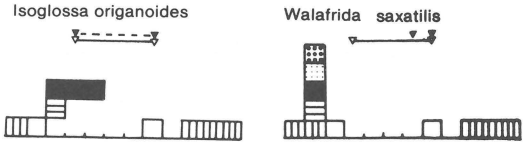
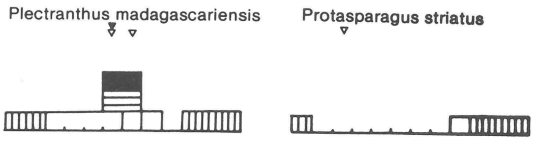


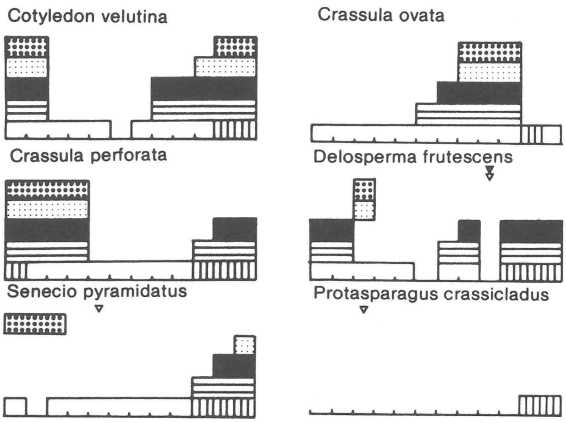
Dwarf and Low Deciduous Shrubs



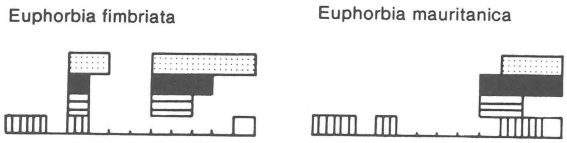
Dwarf and Low Evergreen Shrubs



Dwarf and Low Leaf Succulents



Dwarf and Low Stem Succulents



Appendix 1 Continued

Lianes

Kedrostis nana

Myrsiphyllum asparagoides

Rhoicissus digitata

Rhoicissus tridentata

Sarcostemma viminale

Parasites

Rhoiacarpos capensis

Thesium scandens

Viscum crassulae

Viscum rotundifolium

Addo Bush

Annuals

Chenopodium album

Lepidium africanum

Solanum coccineum

Geophytes

Albuca sp.

Bonatea speciosa

Ornithogalum sp.

Oxalis stellata

Sansevieria hyacinthoides

Perennial Grasses

Cynodon incompletus

Eragrostis obtusa

Mariscus albomarginatus

Panicum deustum

Mid-high and Tall Deciduous Shrubs

Ehretia rigida

Grewia robusta

Pelargonium peltatum

Lycium oxycarpum

Protasparagus suaveolens

Protasparagus racemosus

Protasparagus subulatus

Protasparagus mucronatus

Rhigozum obovatum

Mid-high and Tall Evergreen Shrubs

Brachylaena ilicifolia

Capparis sepiaria

Euclea undulata

Maytenus capitata

Pappea capensis

Putterlickia pyracantha

Schotia afra

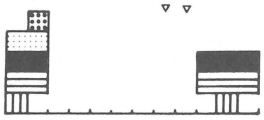
Appendix 1 Continued

Mid-high and Tall Leaf Succulents

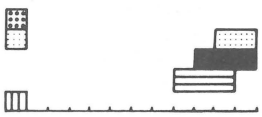
Portulacaria afra

Mid-high and Tall Stem Succulents

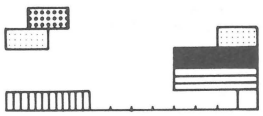
Euphorbia burmannii



Euphorbia ledienii

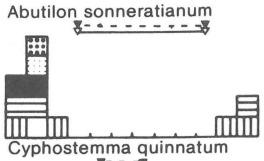


Euphorbia pentagona

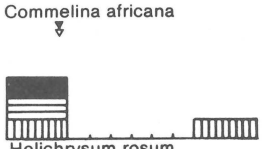


Dwarf and Low Deciduous Shrubs

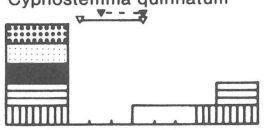
Abutilon sonneratianum



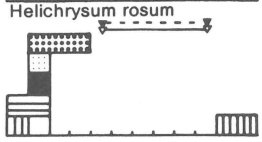
Commelina africana



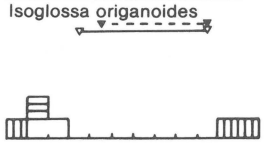
Cyphostemma quinnatum



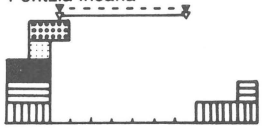
Helichrysum rosum



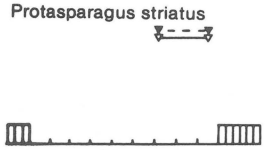
Isoglossa origanoides



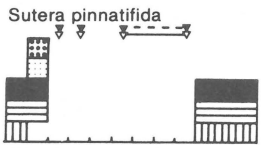
Pentzia incana



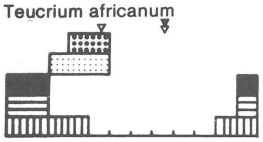
Protasparagus striatus



Sutera pinnatifida



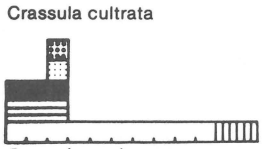
Teucrium africanum



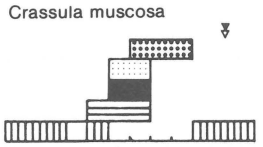
Walafrida micrantha

Dwarf and Low Leaf Succulents

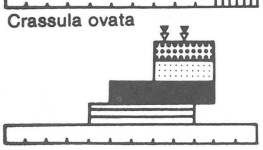
Crassula cultrata



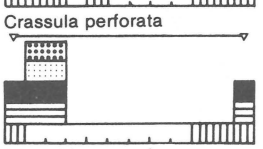
Crassula muscosa



Crassula ovata

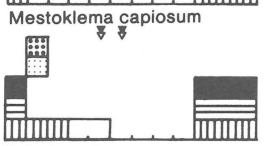


Crassula perforata

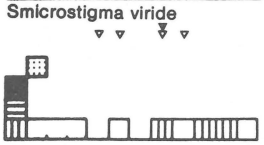


Gasteria maculata

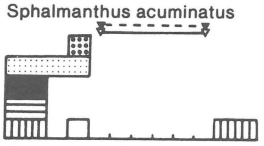
Mestoklema capiosum



Smicrostigma viride



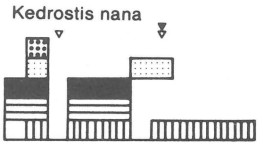
Sphalmanthus acuminatus



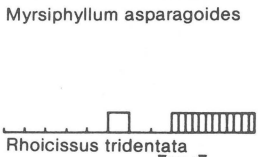
Lianes

Fockea edulis

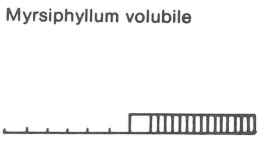
Kedrostis nana



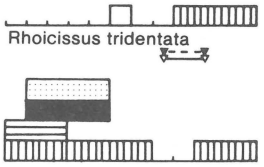
Myrsiphyllum asparagoides



Myrsiphyllum volubile



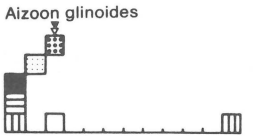
Rhoicissus tridentata



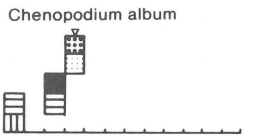
Noorsveld

Annuals

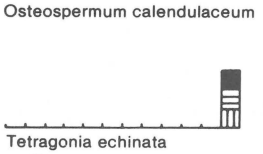
Aizoon glinoides



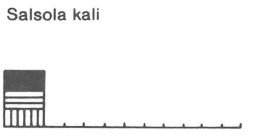
Chenopodium album



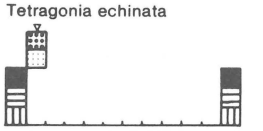
Osteospermum calendulaceum



Salsola kali



Tetragonia echinata



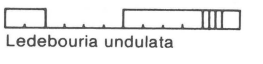
Geophytes

Albuca sp.

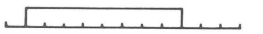
Drimia anomala

Haemanthus albiflos

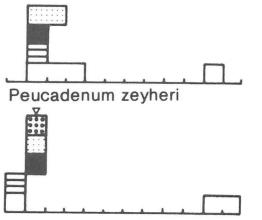
Ledebouria undulata



Moraea polystachya



Peucadenum zeyheri



Sansevieria hyacinthoides

Annual Grasses

Chloris virgata

Setaria verticillata

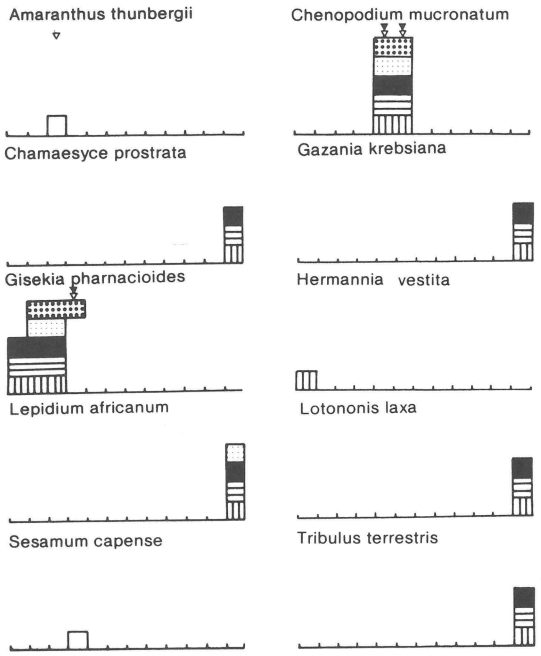
Tragus racemosus

Appendix 1 Continued

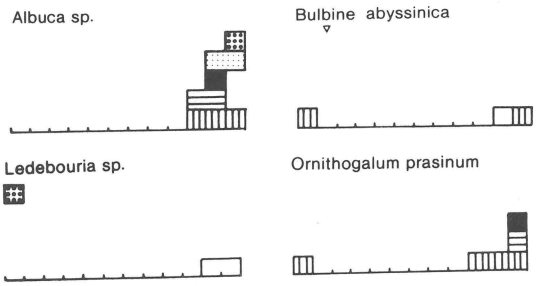
Appendix 1 Continued

Central Lower Karoo

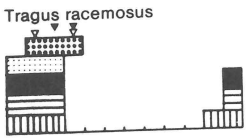
Annuals



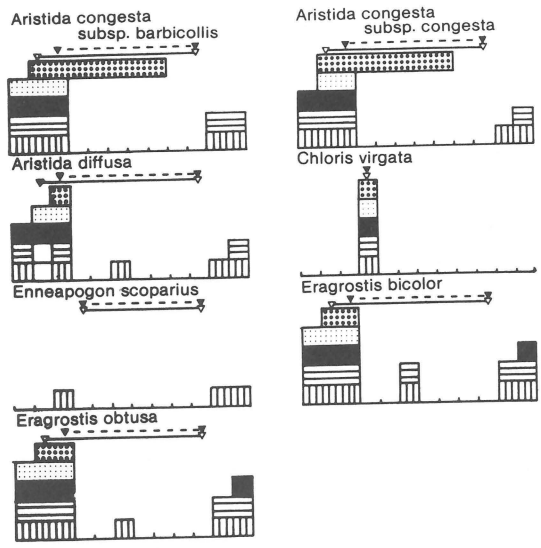
Geophytes



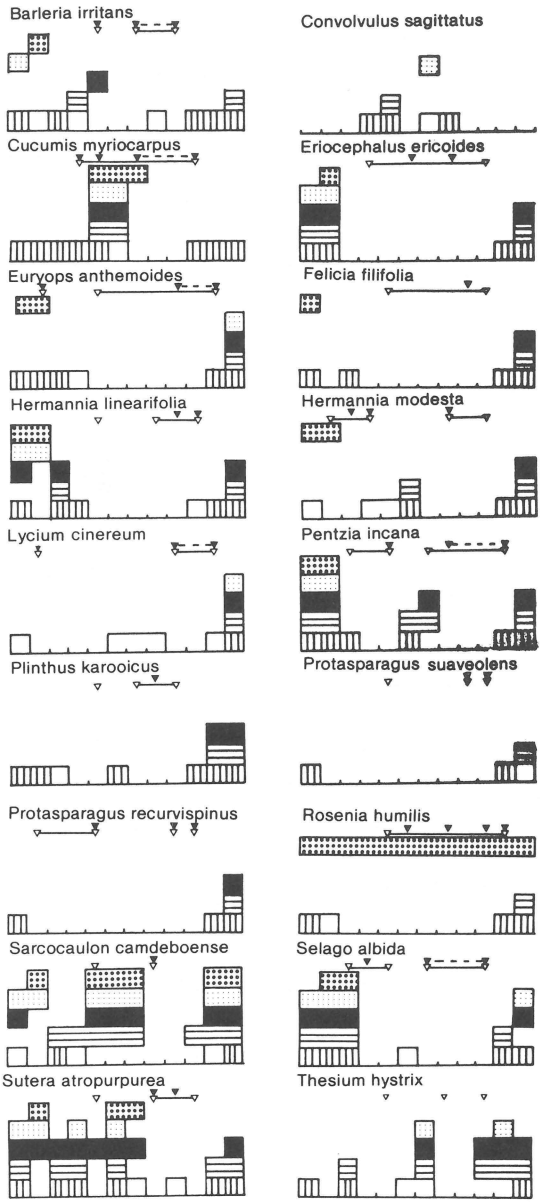
Annual Grasses



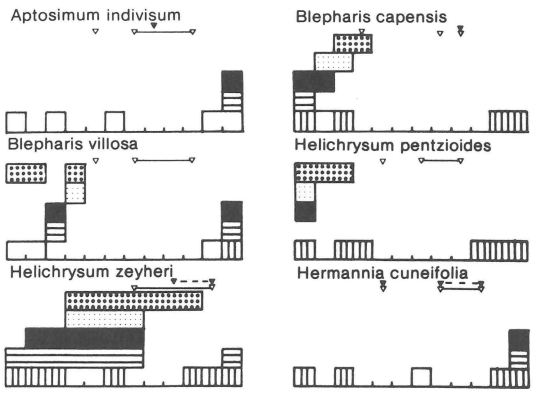
Perennial Grasses



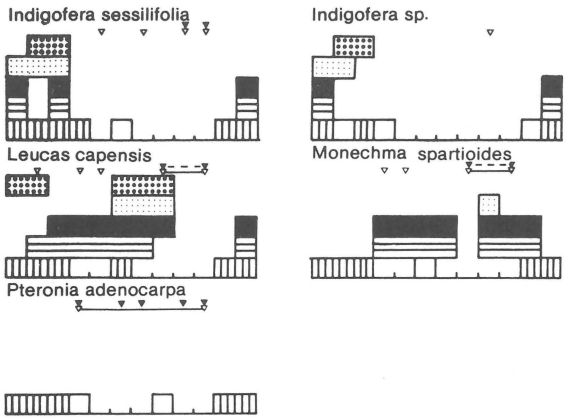
Dwarf and Low Deciduous Shrubs



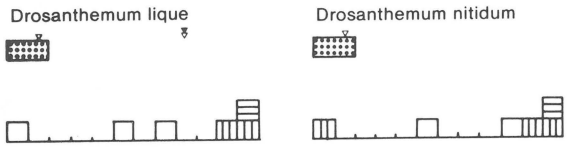
Dwarf and Low Evergreen Shrubs

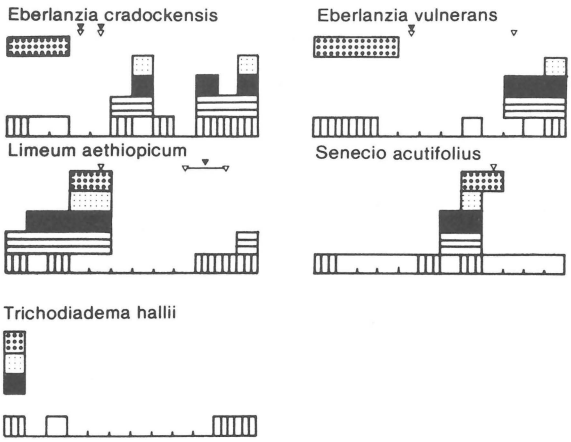


Appendix 1 Continued



Dwarf and Low Leaf Succulents





Dwarf and Low Stem Succulents